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2
Modeling for Endangered-Species Recovery: Gray Wolves in the Western Great Lakes Region

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2.1 Introduction

The Federal Endangered Species Act is intended to conserve endangered and threatened species and their habitats and to improve the species' status so that they no longer need protection under the Act. In the process of planning the recovery of threatened or endangered species, the U.S. Fish and Wildlife Service increasingly uses demographic models to predict population growth and risk of extinction, investigate the factors responsible for species endangerment, and examine the relative effectiveness of alternative management options for species recovery. Demographic models range from simple matrix models for estimating population change (Getz and Haight 1989) to complex, spatially explicit, individual-based models of population dynamics (Dunning et al. 1995). Such models require at a minimum an understanding of the age, stage, and social structure of the population and estimates of reproductive success and survivorship for different life stages. The purpose of this chapter is to describe an example of the construction of a demographic model with application to questions associated with the recovery and management of the endangered gray wolf (*Canis lupus*)population in the western Great Lakes region of the United States.

The most common use of demographic models in recovery planning is the prediction of long-term, range-wide extinction risks, a process called population viability analysis (PVA) [see Boyce (1992a) and Beissinger and Westphal (1998) for review]. An endangered-species recovery plan contains criteria for recovery (i.e., delisting) and reclassification (i.e., change from endangered to threatened status) that specify goals for the size, distribution, and other attributes of the population. The results of a PVA inform recovery planners who set the population goals. For example, Kelly et al. (1999) and Ellis et al. (1999) describe applications of commercial PVA software in recovery planning for the endangered red wolf (*Canis rufus*) and Florida panther (*Felis concolor coryi*) in the southern United States. In other cases, such as the endangered piping plover (*Charadrius melodus*)

(U.S. Department of the Interior 1996), custom models have been built to predict population trends and to help establish recovery targets.

Demographic models have also been developed to address specific questions about the management of an endangered species that arise during the implementation of the recovery plan. These questions usually relate to potential threats, such as habitat destruction or any other natural or man-made factor that might affect the continued existence of the species. For example, Lamberson et al. (1994) analyzed the impacts of habitat patch size and spacing on population viability and thereby helped direct the design of forest reserves for the endangered Northern spotted owl (*Strix occidentalis caurina*).

The modeling projects in this chapter address specific management questions that were raised during the recovery of the gray wolf. The questions involved predicting the impacts of human-caused mortality, changing regional environmental conditions, and disturbance on the persistence of small wolf populations. In addition, the questions involved predicting the relative performance of different strategies for controlling wolf populations. Our approach involved constructing a relatively simple population model that was consistent with the current level of understanding of wolf dynamics and was customized to address specific management questions. Our model included the basic processes of wolf demography (birth, survival, and dispersal) and the social structure of a wolf population. We used the model to simulate population impacts of changes in demographic parameters, and we used model predictions to infer how changes in management activities and environmental processes might affect wolf populations. While we used the same basic population model for all the projects, we modified the model and developed distinct simulation experiments to address each question separately. Our approach differs from other gray wolf modeling projects, such as long-term PVA using commercial software [e.g., Rolley et al. (1999); Kelly et al. (1999); Ewins et al. (2000)] and analytical wolf-prey models [e.g., Walters et al. (1981); Boyce (1992b)], which do not address the population effects of wolf social structure.

2.2 Wolf Biology and Recovery Status

Wolves live in packs and defend exclusive territories (Mech 1970). Generally, packs are family groups consisting of one dominant breeding pair and their offspring (Mech 1970). In the western Great Lakes region, midwinter pack size averages 4 to 8 wolves, about half of which are pups (Fuller 1989). Because of territoriality, regional population density and reproductive rate depend on the number and size of territories. Wolves are not habitat specific, instead they can live wherever they find enough to eat (primarily ungulates), provided killing by humans or disease is not excessive (Fuller 1995; Mech 1995). Population turnover rates are naturally high,

with six pups born per pack and more than half of pack members lost to mortality and dispersal each year (Mech 1970; Cochrane 2000). A dispersing wolf may pair with one of the opposite sex and colonize a vacant territory or may join another pack and replace a missing breeding member (Mech 1970; Rothman and Mech 1979). A wolf population can cover thousands of square kilometers with several independent but interacting packs. In the western Great Lakes region (Minnesota, Wisconsin, and Michigan), midwinter pack territories average 150 to 180 km^2 (Fuller et al. 1992). Range expansion is facilitated by great variation in dispersal behavior: some wolves establish territories and mate near their natal territories, whereas others move long distances (Gese and Mech 1991).

Although gray wolves once lived throughout the Lake States, European settlers nearly eliminated wolves through intensive, unregulated exploitation. By 1960, wolves were limited to the wilderness of northeastern Minnesota, contiguous to a large Canadian wolf population, and Isle Royale in Lake Superior (Mech 1970). Following protection under the U.S. Endangered Species Act in 1973, wolf numbers and range in the Great Lakes region increased. Yet in the core wilderness range within the Superior National Forest, Minnesota, precipitous local extirpation of white-tailed deer (*Odocoileus virginianus*) caused a sharp decline in wolf numbers in the 1970s until the remaining wolves switched to hunting less numerous moose (*Alces alces*) (Mech 1986). The wolf decline was thought to be spreading westward into Voyageurs National Park in the mid-1980s (Gogan et al. 2000). Thus, while wolves were generally faring well by the 1980s, their long-term persistence was still not certain throughout the western Great Lakes region.

After determining that most wolf mortality near Voyageurs Park was caused by humans, either accidentally or by deliberate illegal killing, biologists raised concerns about recreational disturbance impacts on the park's wolves. Interagency consultation with the U.S. Fish and Wildlife Service on park development proposals in 1992 led to stipulations for a cumulative effects model to assess the long-term fate of wolves in the park (Cochrane 2000). At the same time, wolves had moved into the largely forested region of northern Wisconsin, but their fate was uncertain because they had colonized isolated areas with relatively low road densities within a human-dominated landscape. To meet recovery goals in Wisconsin and Michigan's Upper Peninsula, wolves would have to be able to survive in nonwilderness conditions. Modeling was seen as a useful approach to explore wolf viability in human-dominated landscapes (Haight et al. 1998).

By the late 1990s, the picture for wolves was much more favorable, with their range covering most of northern Minnesota, northern Wisconsin, and upper Michigan (Figure 2.1). In 2000, the population in Minnesota exceeded 2400 wolves (W.E. Berg and S. Benson, Minnesota Department of Natural Resources, personal communication, 2000), and the populations

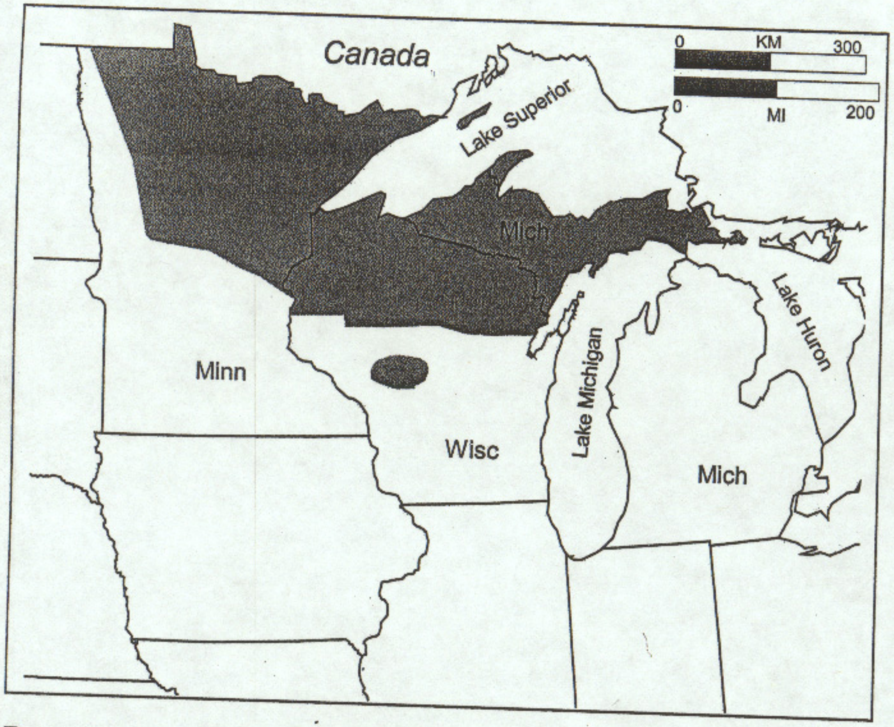

FIGURE 2.1. Shaded areas show the approximate range of gray wolves in Minnesota, Wisconsin, and Michigan in the year 2000.

in Wisconsin and Michigan each exceeded 200 wolves (U.S. Department of the Interior 2000). The great increases in wolf numbers and range raised new issues about controlling negative impacts from wolves, including depredation on livestock and pets, which could be explored through modeling (Haight and Mech 1997).

Because of the growth and recovery of wolf populations in the Lake States, the U.S. Fish and Wildlife Service has proposed reclassifying the gray wolf from endangered to threatened in the western Great Lakes region. Full removal of this population from the federal list of endangered and threatened species is expected to follow within a few years. When the gray wolf is delisted, responsibility for wolf management will be transferred from the federal government to the states. To facilitate federal delisting and to guide state governments as they prepare to assume wolf management responsibilities, state agencies developed management plans with the primary goal of ensuring the long-term survival of the wolf while addressing concerns about wolf range expansion into agricultural areas and animal damage control. The modeling projects we describe addressed specific questions about managing wolves during the recovery process.

2.3 Case Studies

During the period of wolf recovery in the 1990s, we worked with decision makers and biologists to define and address five wolf management questions, in this order:

1. What conditions support or hinder the persistence of disjunct wolf populations in human-dominated landscapes (e.g., newly colonized habitats in Wisconsin)?
2. What are the cumulative effects of regional environmental conditions and human-caused mortality on wolf population size in a small park (e.g., Voyageurs National Park)?
3. How much disturbance does it take to cause reductions in a small wolf population?
4. Is vasectomy a practical alternative for controlling or reducing the size of a disjunct wolf population?
5. What wolf removal strategies are most effective and efficient for reducing wolf depredation on livestock?

Our management questions involved predicting the impacts of human-caused mortality, regional environmental conditions, and disturbance on the persistence of wolf populations. In addition, the management questions involved predicting the relative performance of different strategies for controlling wolf population size and depredation. We decided not to model these environmental processes and control strategies directly. Rather, we made a demographic model of wolf population dynamics and made assumptions about how these environmental processes and control strategies affected the birth, survival, and dispersal of wolves. Then, we used the model to investigate the population impacts of changes in these demographic parameters. Finally, we interpreted the model results as inferences of the population impacts of the environmental processes and control strategies.

We constructed the wolf population model to represent key elements of wolf demography and social organization. Because wolves live in packs and defend territories, we decided to represent a wolf population as a collection of packs and to model the demography of each pack. Within a pack, only one female breeds each year, and mortality rates are age dependent. Furthermore, we were interested in the population impacts of human activities that affected breeding. Thus, we decided to use a stage-structured model that kept track of the age, sex, and breeding status of wolves in each pack. Juvenile and adult wolves disperse from natal packs in search of mates and territories. Because of the great variation in dispersal behavior, we decided to use a random dispersal process and did not represent territories as specific shapes on an actual landscape.

In the sections below, we first describe the structure and parameters of the wolf population model and then describe its application to the management questions.

2.3.1 *A Gray Wolf Population Model*

We developed a demographic, stage-structured, stochastic simulation model of wolf dynamics. The model was designed to simulate a wolf population living in a human-dominated landscape with abundant, well-distributed prey. The landscape was bounded by the assumption that it could support a maximum of 64 pack territories. Each territory was classified based on the dominant land use (e.g., agriculture or wilderness). The number of territories and the land-use classifications varied with the objectives of the application.

To simulate wolf life history, we created a stage-class model for the dynamics of each pack. The model used stochastic difference equations with a 1-year time step to simulate the mortality, dispersal, and birth of wolves and the fate of dispersing wolves. Detailed lists of model assumptions and demographic parameter values are given in specific applications in Haight and Mech (1997), Haight et al. (1998), and Cochrane (2000). For illustration, we describe the parameter values used to predict the performance of alternative wolf removal strategies for population size control (see Section 2.3.6). These parameter values represent 5- to 10-year averages of observations in north central Minnesota (Fuller 1989) and Wisconsin (Wydeven et al. 1995).

Each pack was characterized by the number of wolves of each sex in each of four stages, which were defined based on age and breeding status. Three age classes for nonbreeding wolves were pup (0 to 12 months), yearling (12 to 24 months), and adult (>24 months). The fourth stage was defined for the breeding pair, each of which must be at least 12 months old by the first of May. Because breeding was assumed to take place in March, the minimum breeding age was 22 months.

The annual cycle of events (Figure 2.2) began in autumn with the tally of population attributes, including population size and the number of packs. The first demographic event was mortality in autumn and winter, which represented losses from natural and human (accidental and illegal) causes. The number of wolves that died in each life-history stage was a binomial random variable with a mean that depended on wolf age. Pups were subject to a 65% mortality rate, while yearlings and adults had a 32% mortality rate. In other applications, the age-dependent mortality rates varied from pack to pack, depending on the land-use class (e.g., adult mortality rates were lower in packs in wilderness areas compared with packs in agricultural areas because there was less human-caused mortality).

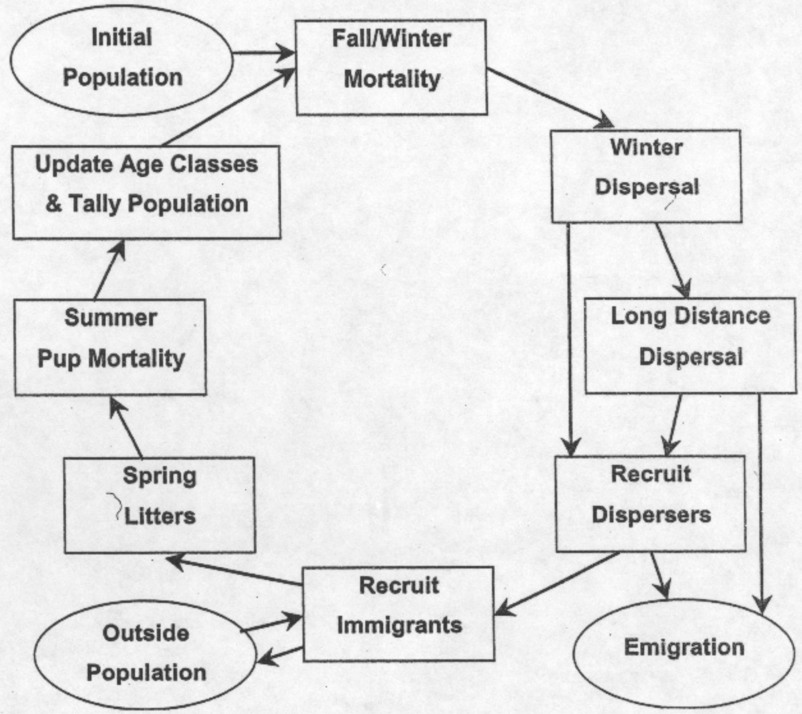

FIGURE 2.2. Annual sequence of events in the gray wolf population model.

Dispersal took place in late winter and depended on the survival of the breeding pair. If the breeding pair died, remaining pack members dispersed. If one or both breeders were present, the number of dispersers from each age class was a binomial random variable. Dispersal probabilities for pups, yearlings, and nonbreeding adults were 25, 50, and 90%, respectively, so that most nonbreeding wolves dispersed before reaching 4 years old (Gese and Mech 1991). We assumed that 20% of the dispersing wolves were long-distance dispersers that immediately emigrated from the area and thus were lost from the population, based on studies demonstrating this type of rapid, long-distance dispersal behavior in Minnesota wolves (Gese and Mech 1991).

Each remaining disperser searched the area for a suitable site, which was defined as a vacant site or a site with an available mate. Wolves could only settle into territories by mating or becoming a territory-holding, available breeder. To account for immigration from a population outside the area, we assumed that six outside wolves joined this pool of dispersing wolves in the search for suitable sites. Each dispersing wolf and immigrant was assumed to sample six territories at random with replacement [see Lande (1987) and Lamberson et al. (1994) for other applications of this kind of search model]. The implication of this assumption was that spatial coordinates and shapes of pack territories were not included. The probability of finding a suitable site was one minus the probability of failing to find a suitable site within six trials:

$$P = 1 - [(1 - S)/T]^{\wedge}N$$

where P is the probability of success, S is the number of suitable sites, T is the total number of sites, and N is the number of trials.

A uniformly distributed random number was drawn for each dispersing wolf and compared with the probability of success. A successful wolf was randomly assigned to a site with an available mate, and if no mate was available, to a vacant site. An unsuccessful wolf was assumed to be lost from the population (e.g., the wolf died or emigrated). Thus, whether or not dispersing wolves settled into a territory and remained in the population depended on the number of suitable sites.

A new litter of pups was born in spring if a breeding pair was present. Litter size was chosen from a discrete probability distribution with a mean of 6.5 pups and a range of 0 to 10 pups (Fuller 1989). The sex of each pup was a Bernoulli trial with equal probability. If there was only one member of the breeding pair present, the wolf held its territory but did not produce a litter. Nonbreeding pack members could not mate without first dispersing from their natal pack. Recent evidence suggested that parent–offspring or sibling mating rarely, if ever, occurs (Smith et al. 1997).

Summer pup mortality was modeled as a binomial random variable with a mean depending on the modeled scenario, such as incidence of disease or prey biomass available. Instead of defining a separate process for the summer mortality of older wolves, we assumed that any older wolves that died in the summer were accounted for in the winter mortality process, which was based on annual mortality rates.

Following birth and summer pup mortality, the age distribution of each pack was updated, and population statistics were tallied, representing a typical autumn population census. The number of wolves by life stage of each pack was used as the basis of the next annual cycle.

Using the demographic parameters described above, we tested the model by comparing the growth rate of a simulated colonizing population with the actual recolonization of wolves in northern Wisconsin. The Wisconsin population grew from an estimated 34 wolves in 1990 to 248 wolves in 2000, an average annual growth rate of 22% (U.S. Department of the Interior 2000). The simulated population started with 40 wolves in 4 packs and grew to 244 wolves in 38 packs in 10 years, an average annual growth rate of 20%.

We also checked the model's prediction of the relationship between population growth and mortality (Haight et al. 1998). The rates of population growth and mortality observed over 5 to 10 years have been compiled from wolf population studies throughout North America (Fuller 1989) and show a strong negative correlation. Using a colonizing population of 40 wolves in 4 packs, we simulated the 5-year population growth under different adult mortality rates (10 to 50%). The rates of population growth were negatively correlated with mortality and suggested that population size stabilized with a mortality rate of about 35%, similar to the conclusion of Fuller (1989) based on field studies. Additional model tests and sensitivity analyses are reported in Cochrane (2000).

The software for the wolf simulation model was written by and is available from the two senior authors. Versions of the source code were written in FORTRAN and Visual BASIC. The applications were performed on an IBM300PL and other personal computers. We have used this type of model for other social carnivores, including the San Joaquin kit fox (*Vulpes macrotis mutica*) in California (Haight et al. 2002) and the African lion (*Panthera leo*) (Starfield et al. 1981). Population models with similar territorial and dispersal mechanisms were used for northern spotted owl (*Strix occidentalis caurina*) recovery planning (Lande 1987; Lamberson et al. 1994).

2.3.2 Persistence of Wolves in Human-Dominated Landscapes

Following protection under the Endangered Species Act in 1973, wolves from northeastern Minnesota recolonized most of northern Minnesota and parts of northern Wisconsin and northern Michigan (see Figure 2.1). The landscape in this range was not wilderness but a mosaic of forest, agricultural, and developed land under a variety of public and private ownerships (Mladenoff et al. 1995). Logging and agriculture had created extensive areas of young forest that supported large populations of white-tailed deer, the preferred prey of wolves in this region. Colonizing wolves first settled in forested areas with few roads and little human settlement. Later, wolves settled in forested areas with higher road and human population densities (Fuller et al. 1992). The wolf populations in Wisconsin and Michigan were separated from the larger source population in northern Minnesota by large areas of less-favorable habitat and Lake Superior. Further, much of the wolf mortality was human caused, whether intentional, accidental, or indirectly caused through the transmission of disease from domestic dogs (Fuller et al. 1992).

Because the management objectives of state agencies included protection of colonizing wolf populations, the agencies wanted to predict the fates of small, disjunct populations under alternative assumptions about human-caused mortality. To address this question, Haight et al. (1998) used the wolf model to simulate a hypothetical disjunct wolf population. The model assumed a maximum of 16 wolf territories divided into core and peripheral ranges. The average annual mortality rate in the core range was 20%, whereas the mortality rate in the peripheral range was higher (40%) because of human-caused deaths. Haight et al. (1998) conducted a set of simulation experiments in which they varied the proportion of the 16 territories in core and peripheral ranges and observed the 50-year occupancy of that range by wolf packs. In the sensitivity analysis, they repeated this set of experiments under different assumptions about pup and dispersal mortality and immigration.

These sets of simulations supported a favorable outlook for the survival of small, disjunct wolf populations like those in northern Wisconsin and Michigan. The results showed that the level of occupancy increased as the number of core sites and immigrants increased. With pup and dispersal mortality rates that were consistent with disease-free and legally protected populations, the model predicted that wolves would saturate a cluster of 16 territories with as few as two core, low-mortality sites, regardless of immigration rates. When pup and dispersal mortality rates were high, as few as two immigrants per year helped maintain site occupancy in clusters with four or more core sites.

These simulation results were consistent with observations of disjunct wolf populations in the United States and Canada (Fritts and Carbyn 1995). For example, during the past 60 years, a population of 40 to 120 wolves has lived in and around Canada's Riding Mountain National Park (3,000 km^2). The park is surrounded by agricultural land, and the nearest wolf population is 45 km away. The population survived even though many of the packs were vulnerable to human exploitation along the park boundary. Based on empirical evidence and simulation results, Haight et al. (1998) concluded that wolves can survive and thrive in networks of disjunct populations, provided that they are linked by dispersal, human persecution is not excessive, and prey are abundant. Further, they concluded that, with continued protection from deliberate killing, wolf range will expand in human-dominated landscapes where prey are abundant. These predictions were incorporated into wolf recovery and management plans written by state agencies. The results also raised questions about the need for population control, especially where wolf presence conflicts with other valued land uses.

2.3.3 External Threats to Gray Wolves at Voyageurs National Park

Voyageurs National Park is a small (882 km^2) reserve of boreal and mixed-deciduous forests and numerous lakes in the heart of wolf range on Minnesota's Canadian border. In the 1990s, park biologists were concerned that high levels of human-caused mortality among wolves immediately surrounding the park could combine with changing prey densities and disease incidence to reduce or even threaten park wolves. Following inter-agency consultations to evaluate the impacts of proposed park recreation development, park biologists commissioned use of a cumulative effect model to address their concerns. Rather than build the comprehensive,

habitat-based model envisioned by park biologists, Cochrane (2000) used the demographic wolf population model to predict the relative effects of four environmental factors (prey availability, human-caused mortality, immigration, and disease mortality) on the persistence of wolves in the park.

To predict the relative impacts, Cochrane (2000) employed a full-factorial experimental design with the four environmental factors at five levels each. The wolf population in the model was assumed to occupy a maximum of 15 territories, 3 inside the park and 12 surrounding the park. The response variable was the likelihood that wolf population size inside the park fell below specified thresholds in any year before the 30-year time horizon. Ten response variables were measured with population sizes from 0 to 18 wolves in increments of 2. The level for each primary environmental factor was specified in terms of the levels of one or more demographic parameters in the simulation model. The level of prey availability affected mean litter size and the rates of dispersal and winter mortality; human-caused mortality affected the rate of winter mortality in territories outside the park; and disease mortality affected the rate of summer pup mortality. The levels of immigration were 0 to 24 immigrants per year in increments of 6.

The results of this factorial analysis (Figure 2.3) suggested that disease mortality is the most important factor affecting whether or not the park wolf population would remain near its initial population size. Immigration had the most impact on the likelihood that the wolf population in the park would fall below a threshold of seven wolves. Human-caused mortality in wolf territories outside the park had little effect on the number of wolves in the park, except when the population was already very small under extreme conditions of no immigration, very low prey biomass, and high disease mortality. While changes in the demographic parameters associated with alternative levels of prey availability had little effect on wolf population size, prey availability had stronger effects in experiments where prey determined territory spacing or sizes (results not shown). Thus, prey availability within foreseeable ranges had an effect on total wolf numbers (through the number of territories that can "fit" within the small park) but very little relationship with the likelihood of extirpation. It was easier to maintain breeding pairs rather than a large population in the park, and these breeding pairs were highly resilient to extirpation because of the readily available pool of replacement breeders.

The results of this factorial analysis helped ameliorate concerns about human-caused mortality of wolves outside the park while focusing new attention on the spread of disease from dogs to wolves. In addition, the model results indicated which environmental conditions would likely enhance the security of the population. Those environmental conditions, which supported the population's reproductive capacity more than a constant, large population size, could be monitored in lieu of intensive wolf population sampling or trend interpretation.

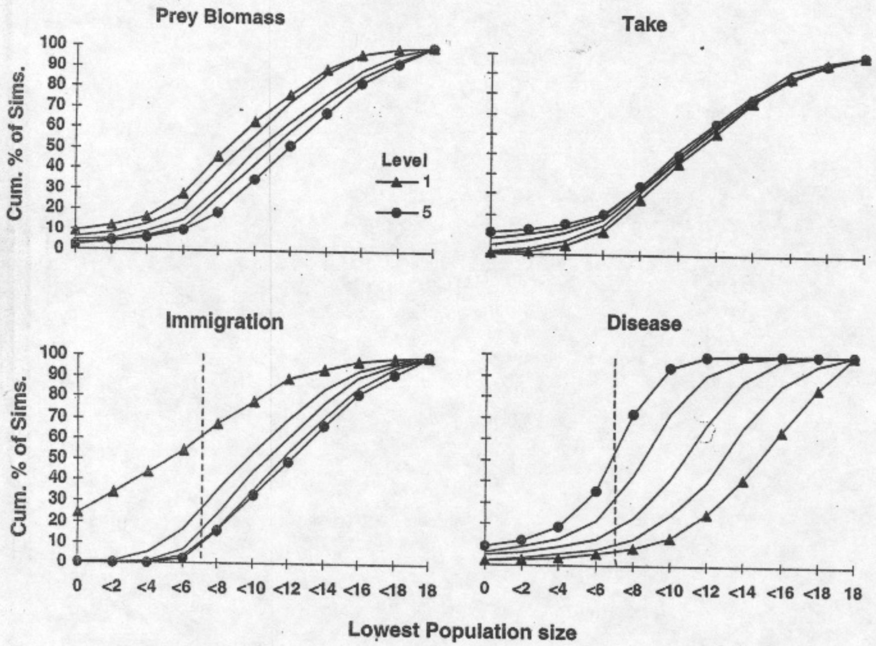

FIGURE 2.3. Proportions of simulations that fell below different wolf-population-size thresholds in Voyageurs Park out to a 30-year horizon. Each graph shows outcomes associated with one cumulative impact factor at five different levels from the lowest (Level 1) to the highest (Level 5) level tested. "Take" refers to human-caused mortality. The initial population included 18 wolves in the park.

2.3.4 Disturbance Effects on Gray Wolves inside Voyageurs National Park

In addition to human-caused mortality of wolves outside Voyageurs National Park, biologists were concerned about the impact of humans on the behavior of wolves inside the park. For example, when disturbed by humans, wolves sometimes move pups to alternative den sites and temporarily ignore prey. While examples of these responses to humans have been observed in protected areas, their frequency and impact on wolf demography at this park are not known. Cochrane (2000) used the wolf population model to investigate how altered behavior of individual wolves or packs, expressed as temporary changes in the demographic parameters in the population model, might affect the persistence of wolves in the park. The purpose was to provide park biologists with guidance on the magnitude and frequency of disturbance events that could affect wolf population size.

To predict the relative impacts of different types of disturbances, Cochrane (2000) simulated a wolf population that was assumed to occupy

a maximum of 15 territories, 3 inside the park and 12 surrounding the park. The demographic parameters represented current regional conditions for prey biomass, human-caused mortality, wolf disease, and immigration.

Cochrane (2000) defined 125 disturbance scenarios based on type of disturbance event and frequency of occurrence within the park. The five types of disturbance events were loss of one, two, and three wolves; loss of an entire litter; and displacement of an entire pack from its territory. The 25 frequency classes had average intervals between events from 1 to 100 years. Each disturbance scenario was simulated 1000 times, and the response variables were the average size of the wolf population in the park after 30 years and the likelihood of falling below population-size thresholds, as in the previous study.

The disturbance events had little effect on population size when the number of years between events averaged 6 years or more (Figure 2.4). When disturbances occurred with an average return interval of less than 6 years, scenarios involving losses of litters resulted in the smallest wolf populations. The results in Figure 2.4 can be used to inform the development of management guidelines for controlling disturbance events. For example, to obtain a population of at least 24 wolves after 30 years, a litter of pups cannot be lost more often than once every 6 years. The results in Figure 2.4 are projections of average responses to simulated disturbance events under current conditions, and we explained to park managers that they should not expect to see such a specific or precise impact, given the diverse factors affecting park wolves at any time.

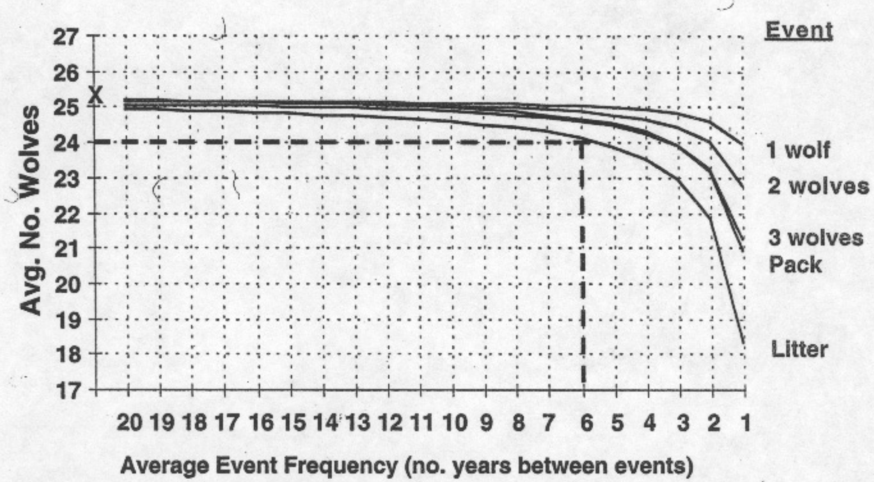

FIGURE 2.4. Predicted relationships between the average number of wolves in Voyageurs Park after 30 years and the frequency of disturbance events. The five types of disturbance events were loss of one, two, and three wolves; loss of an entire litter; and displacement of an entire pack from its territory.

These modeling results must be linked to field research to resolve what human activities cause the kinds and frequencies of disturbance that we considered. Generally, if the primary management goal is maintaining wolf numbers, then management actions should focus on protecting the integrity of territories for sustainable use by breeding pairs rather than protecting individual animals from human harassment. This quantitative analysis did not address alternative and largely implicit goals of protecting wolves from any behavioral changes caused by human disturbance or displacement within a natural ecosystem (e.g., Forbes and Theberge 1996).

2.3.5 Vasectomy for Wolf Control

In the late 1990s, recovering wolf populations in Minnesota, Wisconsin, and Michigan prompted state management agencies to consider strategies to control wolf population growth. Population control may be necessary where wolves colonize areas close to human settlement and conflict with other valued land uses. Because killing wolves to control population size is not acceptable to many people, vasectomy was proposed as a nonlethal control strategy that might have wider public acceptance.

Vasectomy involves sterilizing a male wolf in the field with chemical sclerosing agents to harden and block the sperm tract without affecting hormones. The primary reason that vasectomy might be practical for controlling wolves is that single pairs of adult wolves occupy large territories (150 to 180 km^2 in the western Great Lakes region) and thus control the number of offspring over a large area for 5 years or more. Pairs that fail to produce young because of vasectomies or natural reasons may continue to hold territories for years (Hayes 1995; Mech et al. 1996). Thus, by sterilizing the breeding male in a territory, theoretically a manager could restrict the number of wolves in that large area for years.

To evaluate and compare wolf control strategies, Haight and Mech (1997) used the wolf population model to predict the effects of both vasectomy and removal on the trends of a small, disjunct population. The hypothetical population occupied a landscape composed of a maximum of 16 wolf territories equally divided between core (20% annual mortality rate) and peripheral (35% annual mortality rate) ranges. The wolf management strategies included periodic sterilization of all breeding males, sterilization of fertile males caught in a random-trapping design, and various wolf removal designs. Of particular interest was the effect of immigration from neighboring unmanaged populations on the performance of the strategies in the managed population.

Simulations suggested that the effects of wolf vasectomy in a small, disjunct population are strongly related to the level of annual immigration. With low immigration, periodic sterilization reduced pup production and resulted in lower rates of territory recolonization. Consequently, average pack size, number of packs, and population size were significantly less than those for an untreated population. With high immigration, periodic sterilization reduced pup production, but not territory recolonization and, therefore, resulted in only moderate reductions in population size relative to the untreated population. While periodic wolf removal produced the same population size trends as sterilization, more than twice as many wolves had to be removed than sterilized.

While sterilizing free-ranging wolves for population control has never been attempted, the simulation results of Haight and Mech (1997) suggested that for small, disjunct wolf populations, such as those that inhabit much of Wisconsin, Michigan, and central Minnesota, vasectomy may be a practical, cost-effective method of controlling wolf numbers. The method would require handling fewer wolves than would lethal trapping, although sterilizing captured wolves would require more highly trained workers.

Whether vasectomy would be effective or practical in larger populations is unknown. The simulation results of Haight and Mech (1997) suggested that, when turnover in breeding tenure is high, vasectomy is less effective. However, lethal methods would also be less effective in such populations. Thus, experimentally comparing sterilization and lethal control appears to be worth trying even in larger populations.

2.3.6 Wolf Removal Strategies for Animal Damage Control

Wolf management planners in Minnesota, Wisconsin, and Michigan must develop strategies that balance competing demands for wolf protection and animal damage control. As wolf populations in these states increased in the 1990s, wolf range expanded into areas with farms and livestock, and wolf depredations on livestock and domestic animals increased. For example, from 1979 to 1988, an average of 26 Minnesota farms were affected, and 32 wolves were destroyed annually; from 1989 to 1998, an average of 66 farms were affected, and 126 wolves were destroyed each year (Mech 1998). As a result, many farmers and rural residents expressed concern about expanded wolf range and increased animal damage, calling for population controls or sport harvest seasons. At the same time, wolf protection advocates argued that depredation control should continue as a government program but without a general harvest or limitations on wolf range and population expansion.

Given these conflicting demands for wolf management in agricultural regions, we used the wolf population model to evaluate and compare the performance of three types of wolf removal strategies that were considered by state management agencies as candidates to balance those demands. The removal strategies included reactive management, in which wolves were removed from territories following recent depredation; preemptive management, in which wolves were removed from territories in which depredation had occurred in 1 or more of the previous 5 years; and population control, in which wolves were removed from all territories overlapping livestock production areas regardless of the depredation history. We simulated a hypothetical 64-pack wolf population living in a landscape composed of equal proportions of farm and wild areas. The simulations were used to predict the relative performance of the three strategies taken alone and in combination. The model predicted the number of wolf depredations on livestock and the number of wolves removed out to a 20-year horizon.

The most significant result was that, compared with no action, each removal strategy alone cut depredation in half (Figure 2.5). Depredations were reduced because each strategy focused on wolf removal in territories overlapping farms. As a result, many farm territories were free of wolves during the spring and summer, when depredation occurs. While wolf removal focused on farm territories, wolves were not removed from wild areas within the simulated region. As a result, the population was never in danger of extirpation. The number of removals varied greatly among strategies and depended on the timing of removals. Under preemptive management, wolves were trapped and removed in winter before pups were born. As a result, preemptive management removed far fewer wolves than reactive removals or population control in which wolves were trapped and removed after pups were born (see Figure 2.5). Further reductions in depredation were obtained by using two removal strategies each year, which increased the number of farm territories that were free of wolves. If the cost of wolf removal is proportional to the number of wolves removed, the simulation results suggest that preemptive removal of wolves from farm territories in winter is a more cost-effective way to reduce depredations than reactive or population control strategies.

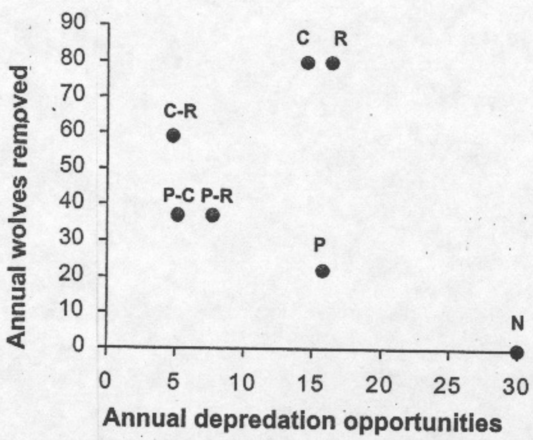

FIGURE 2.5. Predictions of the annual number of wolves removed and the number of depredation opportunities for preemptive (P), reactive (R), population control (C), and no-action (N) strategies. The number of depredation opportunities is the number of wolf packs with territories that overlap farms.

2.4 Lessons Learned

In planning the recovery of an endangered species, models are typically used to estimate the likelihood of extinction and to set minimum viable population sizes for recovery targets. However, as demonstrated by our applications to wolf recovery, models can also be used to address various management questions that arise during the implementation of the recovery plan. In our studies, the management questions involved predicting the potential impacts of human-caused mortality, regional environmental conditions (external threats), and disturbance on the persistence of wolf populations. In addition, the management questions involved predicting the relative performance of different strategies for controlling wolf population size and depredation. As a result of these applications, we learned a number of lessons about management-oriented modeling (Table 2.1). Many of these lessons are consistent with pragmatic guidelines that have been proposed for interdisciplinary modeling projects (Starfield 1997; Nicolson et al. 2002).

A measure of a modeling project's success is the degree to which the results are considered in the development of resource management policy. We found that working in teams that included both expert biologists and managers (Rule No. 1) and carefully defining the management questions (Rule No. 2) was absolutely necessary to fulfill this measure of success. When we involved expert biologists and managers in each phase of model construction and evaluation, the simulation results comparing management strategies and predicting relative effects of environmental factors were credible and informative. Furthermore, by carefully delimiting the management questions, we could better decide and defend which details of wolf demography and behavior were important to include in the model (Rule No. 7).

Our partners understood that the purpose of our modeling exercises was to predict the relative effects of alternative management strategies or different environmental scenarios. Framing our simulation results in relative terms helped our teams gain insights about the management problems, which was more useful and reliable than attempting to predict population attributes precisely under uncertain future conditions (Rule No. 3). Thorough sensitivity analyses were then used to determine how robust the rankings of performance or effects were to changes in uncertain parameters of wolf demography (Rule No. 11). This approach is consistent with an emerging consensus among people involved in endangered-species management that demographic models should be used cautiously in population viability analysis because of concerns about the accuracy of predictions

TABLE 2.1. Heuristics of pragmatic modeling to support management planning.

Rules	Caveats
1. Work as a team with modelers, biologists, and managers	Requires full commitment and good communication skills Continually reaffirm common understanding of objectives and methods
2. The problem must be well defined *first*	Begin from a system or big-picture perspective rather than from the components
3. The purpose of pragmatic modeling is to gain insights and improve management decisions, not to produce precise predictions or absolute answers	Stochastic modeling is well suited to strategic planning (such as setting priorities for regional endangered-species recovery) but is not a panacea for site- and case-specific risk assessments under high uncertainty
4. The project and models must be flexible and adaptable	Be able to change directions (including redirecting funding)
5. Use rapid prototyping and iterative modeling with reevaluation of objectives and process	Rapid turnover of preliminary results to management engages managers in the project and promotes continual focus on modeling relevance and iterative refinement of the objectives and approach Be willing to throw out models that are not working and start over
6. Models must be transparent or easily understood and manipulated	Be careful in using others' models
7. Avoid filling models with extraneous details; err toward simplicity and transparency	Details or variations can always be added if they become important to the objectives
8. Balance what is clearly known with what must be hypothesized	Avoid concentrating on what is already known while ignoring elements that are relevant to the objectives but poorly understood
9. Chose the model scale carefully to match objectives	Generally, scales cannot be blended; if need be, build more than one model at different scales
10. If a simple model does not meet the objectives, consider using a suite of models (each with a well-defined objective)	All-purpose or comprehensive models do not work Modeling experiments built around scenarios can reduce complexity while exploring a wide range of conditions and parameter values
11. Sensitivity analysis is essential	Be explicit about the assumptions and guesses that inevitably must be made to develop a model (virtual-world) representation of the real world Sensitivity analysis tests these assumptions and provides essential perspective

(Beissinger and Westphal 1998). Rather than taking predictions of extinction risk or population size at face value to make a decision, demographic models of population viability are better used to compare the effects of different management options with the goal of setting priorities.

We found it very useful to have a basic model that could be readily adapted to alternative management questions (Rule No. 6), but only because the scale and important factors were similar enough among our projects that it was appropriate to use the same model structure (Rules Nos. 7 and 9). All our projects were concerned with small wolf populations where stochasticity and social population structure influence population densities. Each of our wolf projects asked such distinct questions, however, that different experiments, model adaptations, and output were required.

Our ability to address different management questions was enhanced by developing case-specific versions of our computer code, not a finished package that could be used in multiple ways (Rules Nos. 6 and 10). Our attempt to create a user-friendly version of our model did not work because the model kept changing to meet case-specific needs. The user shell rapidly became obsolete and was not worth the investment. The development of a simpler, educational version of the model may be useful, but this should be a separate project with its own objectives (Rule No. 2).

We contend it would not have been useful to have a "standing" model or box to be pulled out and plugged in to answer these management questions. For the kind of management questions we explored, it was better to keep a modeler involved and working hand-in-hand with biologists and managers than to try to write a model that staff without programming ability could use. We repeatedly revised elements of our modeling experiments beyond the basic model structure. For example in the cumulative effect experiments for Voyageurs Park (see Section 2.3.3), we tested different algorithms for compensation between discrete mortality sources, linked disease to different population segments, considered alternatives with and without density responses in four demographic rates, and so on. In addition, in some of our projects we were able to quickly address questions about model and experimental structures as they arose by producing preliminary results from model prototypes or iterative versions of the model (Rule No. 5). Building a single, general model retaining all these options would have been terrifically cumbersome, more time consuming, and error prone.

Even with our "simple" model, the experiments were at times sufficiently complex to be overwhelming, especially if all assumptions were challenged and tested. We recommend that when modeling exercises bog down in details or complexity or the next step becomes unclear, the modeler should step back and look for ways to simplify the situation and get the next phase started somehow. In other words, cut through the details to keep focusing on what is important (Rule No. 7). Using an iterative or top-down modeling approach (Starfield and Bleloch 1986) was helpful, starting with the most important management issues and environmental factors (Rule No. 2). For example, in the cumulative effect model, we did not include the mechanisms or human actions that drive the demographic variables in the model (Rule No. 7; see also Figure 2.2). Hypothetical scenarios focusing on a limited set of presumed, key factors were a useful way to limit complexity while still exploring a full range of parameter values. Our results indicated that only some of the innumerable environmental and anthropogenic conditions that could be linked to the key factors of wolf population trends merit more detailed investigation.

The Voyageurs Park cumulative effect projects would have benefitted from even greater interaction between park staff and modelers (Rules Nos. 1 and 2). Numerous conditions resulted in initially vague project objectives and priorities: a project mandated by an agency outside the park, a long lead time between project instigation and modeling, staff turnover, and political pressures on park management. Further, we proposed a novel approach to cumulative effect analysis to a staff with limited experience with either modeling or wolves. In retrospect, it would have been helpful to develop some initial analyses or model exercises to connect the new managers to the project and establish more clear objectives for the project from the start.

One of the barriers we experienced with managers was their expectation that the model would "solve their problem" or at least convince constituents that managers were doing the right thing (Rule No. 3). Strategic modeling helps management by revealing the relative importance of different factors and the conditions under which the population is most vulnerable and secure. It may also help identify thresholds for rapidly increasing risk that suggest management criteria. However, modeling does not relieve managers from establishing clear objectives under diverse political pressures or making judgments under uncertainty. Stochastic modeling can provide important insights, but does not tell managers whether or not to prohibit specific human actions or even which management approach is "best" under conflicting societal demands. We had to help managers understand that stochastic population modeling is experimental, not prescriptive. Further, modeling is a process not a product, an interactive, adaptive activity that evolves with the management objectives.

2.5 Conclusions

We illustrated a pragmatic approach to modeling that involved working with expert biologists and managers to construct a simple population model that addressed specific management-oriented questions. The model included the basic processes of wolf demography and social structures necessary to make accurate predictions. Simple simulation experiments were used to determine the population impacts of changes in demographic

parameters, and the results of the experiments were used to infer how changes in management activities and environmental processes might affect wolf populations. This approach to modeling will help address new questions about how wolves are managed in the western Great Lakes region as the population continues to recover and is removed from the Federal Endangered Species List. This modeling approach should also contribute to the recovery and management of other endangered species.

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